

ON THE ORIGIN OF THE ORCHIDACEAE, II¹

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The myriad things in nature are completely similar and completely dissimilar. This should be described as a great similarity in dissimilarity. — HUI SHIH (4th Century B.C.)

IN 1960, in discussing my ideas on the origin of the present-day complexity of the orchid family, I called attention to the presence of five distinct phyletic lines based on the disparity in their respective endomorphic and exomorphic features, as well as on the absolute genetic incompatibility among the members of each line with respect to the others. These kladogenetic lines which have evolved in a parallel manner represent distinct subfamilies known as APOSTASIOIDEAE, CYPRIPEDEOIDEAE, ORCHIDOIDEAE and NEOTTIOIDEAE. The plants referable to these subfamilies are all terrestrial. The epiphytic mode of life evolved through a secondary differentiation which occurred in the NEOTTIOIDEAE, giving rise to a fifth line or subfamily, the EPIDENDROIDEAE (4, 5).

This new departure from the commonly accepted classification into two main divisions — MONANDRAE and DIANDRAE, one *versus* two fertile anthers — has stimulated responses for the continuation of the old *status quo*. The fundamental difference between my thesis and those of my critics is the recognition of the evolutionary lines as natural systematic units, whereas in the opposing approaches, where the phyletic lines are randomly accommodated in some arbitrary categories, the taste and flavor of the ancient numerical system of Linnaeus is still cloyingly prevalent. A summary of the main approaches is given in FIGURE 1.

CRITIQUES AND CRITICAL POINTS

Apostasioideae. An attempt has been made by Vermeulen (13, 14) along the lines which were suggested in the past by Schlechter, Ridley, Takhtajan (12), and more recently by Hutchinson (8) to reinstate the APOSTASIOIDEAE to family status. Yet Stebbins and Khush (11) have convincingly shown that the stomatal complex in the APOSTASIOIDEAE is anomocytic, i.e., two guard cells without subsidiary cells, which is characteristic of the Orchidales. The Haemodoriales or Liliales to which Apostasiaceae has been referred by several is characterized by a paracytic stomatal complex, i.e., two guard cells plus two subsidiary cells. This latter group seems to have arisen only once in evolutionary history of the monocotyledons.

¹ On the origin of the Orchidaceae [I]. Bot. Mus. Leaflet. Harvard Univ. 19: 57-96. 1960.

AUTHOR	MAIN DIVISIONS OF SYSTEM							
LINDLEY		CYPRI- PEDEAE	OPHRYDEAE	ARE - THUSEAE	NEOT- TEAE	MALAXIDEAE	EPIDENDREAE	VANDEAE
BENTHAM	CYPRIPEDIEAE		OPHRYDEAE	NEOTTIEAE		EPIDENDREAE		VANDEAE
REICHENBACH	CYPRIPEDIEAE		OPHRYDEAE	OPERCULATAE				
				NEOTTIEAE		EUOPERCULATAE		
PFITZER	PLEONANDRAE		MONANDRAE					
			BASITONAE	ACROTONAE				
				Acranthae - Convolutae	Acranthae { Duplicatae - Articulatae } Pleuranthae - Sympodiales Monopodiales			
ROLFE	DIANDRAE		MONANDRAE					
			OPHRYDEAE	NEOTTIEAE	EPIDENDREAE			VANDEAE
SCHLECHTER		DIAN- DRAE	MONANDRAE					
			BASITONAE	ACROTONAE				
				Polychondreae	Kerosphaereae			
MANSFELD	DIANDRAE		THRAUOSPHAEREAE			KEROSPHAEREAE		
			OPHRYDEAE	NEOTTIEAE	EPIDENDREAE			VANDEAE
HATCH		CYPRI- PEDIOI- DEAE	ORCHIOIDEAE					
			BASITONEAE	ACROTONEAE				
DRESSLER AND DODSON	CYPRIPEDIOIDEAE		ORCHIDOIDEAE					
			ORCHIDEAE	NEOTTIEAE	EPIDENDREAE			
GARAY	APOSTASI- OIDEAE	CYPRI- PEDIOI- DEAE	ORCHIDOIDEAE	NEOTTIOIDEAE	EPIDENDROIDEAE			
			ORCHIDEAE DISEAE DISPERIDEAE	EPIDOGONEAE NEOTTIEAE CRANICHIDEAE	EPIDENDREAE			VANDEAE
					Phaiinae Dendrobiinae Epidendriinae Pleurothallidinae			Cyrtopodiinae Zygopetaliinae Oncidiinae Vandiinae

FIGURE 1. Summary of various systems of classification of ORCHIDACEAE.

EWS.

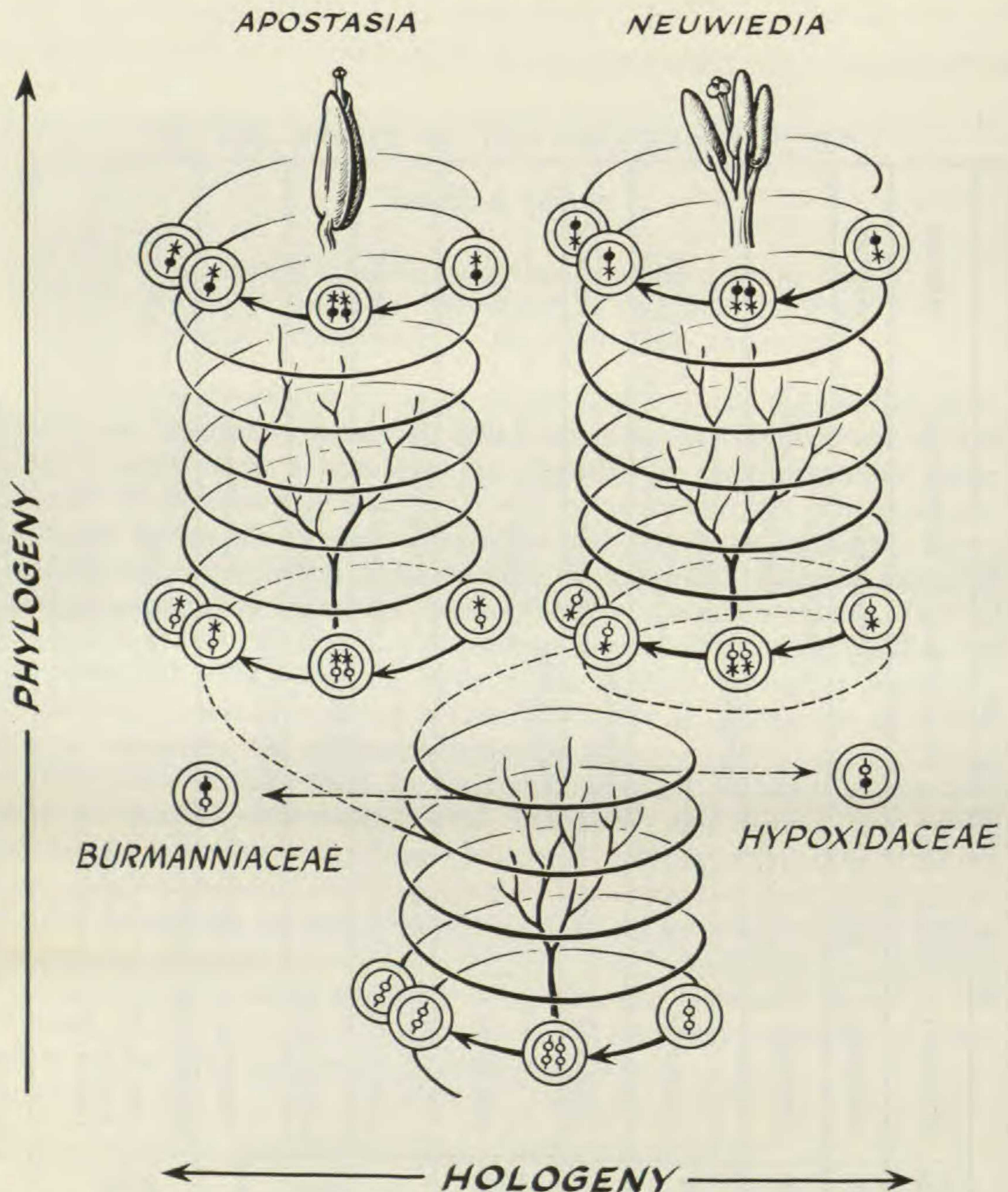


FIGURE 2. Phylogeny and hology of subfamily APOSTASIOIDEAE.

On the other hand Dressler and Dodson (3), Melchior (9), and De Vogel (2) in following Pfitzer consider the APOSTASIOIDEAE merely a tribe under the CYPRIPEDEOIDEAE, notwithstanding the absence of the vaguest superficial resemblance between members of these two subfamilies. As a matter of fact, the two genera that comprise the entire subfamily, *Apostasia* and *Neuwiedia*, are not even closely related to one another but are only relic survivors of ancient anagenetic lines. Their hology is depicted in FIGURE 2 (5). In many ways they resemble the remnants of a grand dinner from which it is no longer possible to reconstruct the complete menu.

Cypripedioideae. This taxon, like the APOSTASIOIDEAE, is a relic group (5, 12). It is composed of four superficially similar genera: *Cypripedium*, *Paphiopedilum*, *Phragmipedium*, and *Selenipedium*. The generic differentiation must have taken place in the obscure evolutionary past, perhaps shortly after the group as a whole was initiated, because of the absolute incompatibility among the members of each line with respect to the other lines. Lack of incompatibility among members of different genera is the rule rather than the exception in the ORCHIDOIDEAE, NEOTTIOIDEAE and EPIDENDROIDEAE (6).

The CYPRIPEIDIOIDEAE has been accepted generally as a distinct subfamily, although its circumscription varies according to the interpreter. Recently Vermeulen, following in the footsteps of Lindley and Mansfeld, but not necessarily following their reasoning, proposed to elevate this group to family status, thus recognizing the Apostasiaceae, Cypripediaceae and Orchidaceae within the order Orchidales (13, 14). Indeed it makes no difference whether or not we recognize five subfamilies or five distinct families so long as the principles that must govern such steps do not become subservient to arbitrary decisions. Such a guide line, however, is wanting in Vermeulen's presentation.

Orchidoideae. In advancing the thesis that the APOSTASIOIDEAE and CYPRIPEIDIOIDEAE must be regarded as distinct families, Vermeulen failed to recognize or appreciate the uniqueness of the ORCHIDOIDEAE, for he included it together with a newly proposed subfamily (although with an old and already known name, EPIDENDROIDEAE) in his new concept of the orchid family (13, 14). It is not difficult to recognize the reason for such an action, for the subfamily ORCHIDOIDEAE includes the genus *Orchis*, the nomenclatorial type of the Orchidaceae. Should one grant family status to each of the five subfamilies, the Orchidaceae will become one of the least significant families in the whole complex, with most of its members showing the strain of ancient isolation and overspecialization (6). The overwhelming majority of the species is in the subfamily EPIDENDROIDEAE. Thus, the interpretation of evolutionary phenomena which led to the idea of the fragmentation of the Orchidaceae into several families has suddenly given way to a completely unrelated aspect of scientific endeavor: nomenclatorial priorities.

The subfamily ORCHIDOIDEAE is composed of well-advanced species, so far without any trace or evidence documenting its origin and progressive differentiation from a lesser evolved stock. The highly evolved pollinia with pollen grains solidly united into massulae which are borne on caudicles with hygrometric behavior (4, 6), the complete basitonic fusion between the anther and the column (4), and the occurrence of polystely in the roots and tubers (15) are all strictly limited to this subfamily.

The column in the ORCHIDOIDEAE is very dissimilar to that found in other subfamilies; the only fertile anther is formed in such a way that it is completely adnate to, and embedded in, the columnar tissue. To derive the column of the NEOTTIOIDEAE and EPIDENDROIDEAE from the ORCHI-

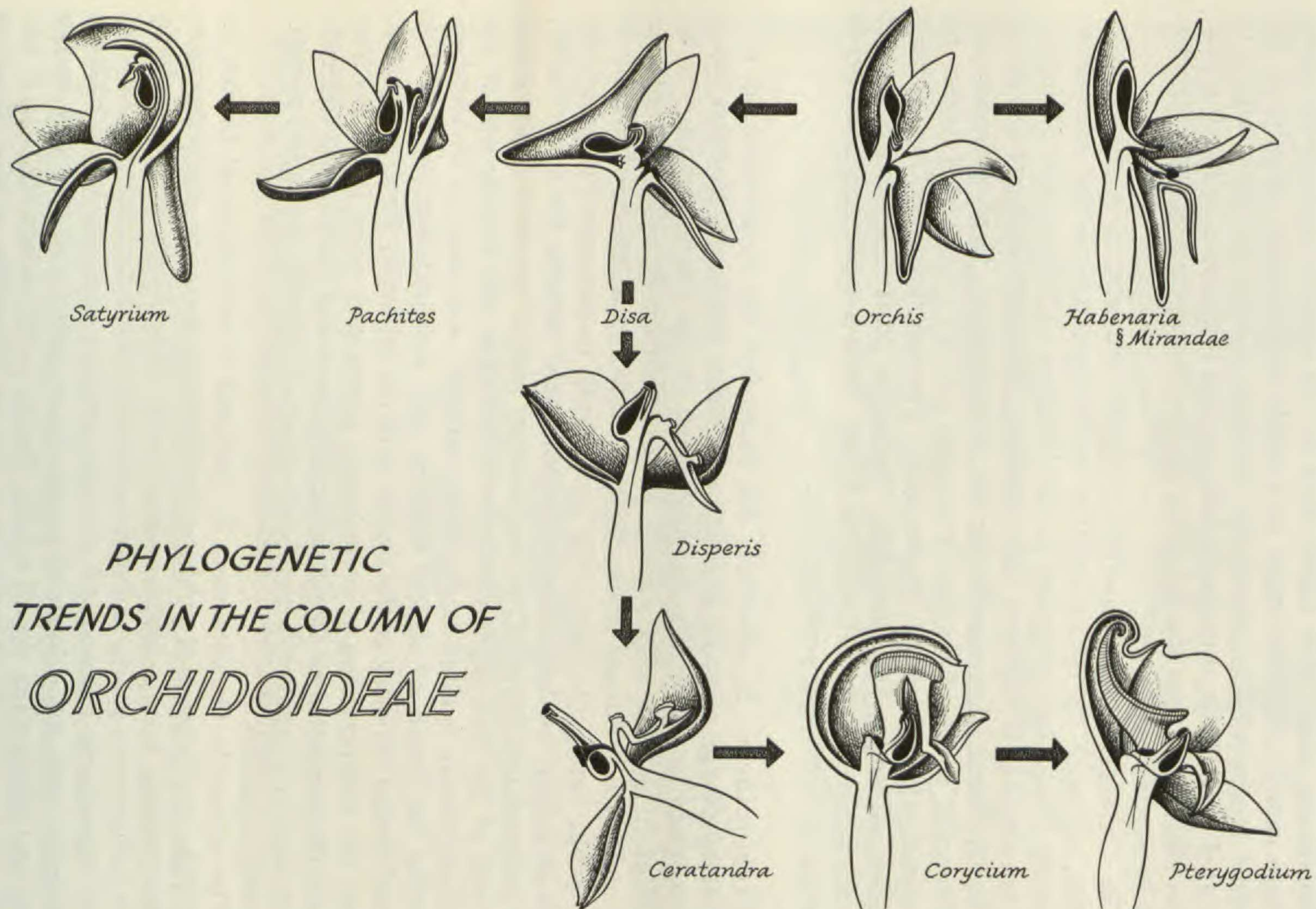


FIGURE 3. Phylogenetic trends in the column of subfamily ORCHIDOIDEAE.

DOIDEAE or *vice versa*, would require the impossible reversal of the true morphological apex of the anther. Although such a reversal may seemingly come about through inclination of the anther, such a directional movement merely changes the position of the true apex without reversing it, as shown in FIGURE 3 depicting that phylogenetic trend (6). It is evident that the various stages in the gyration of the column are intimately correlated with the entomophilous nature of the flowers, each step progressively leading toward irreversible overspecialization, and hence to ultimate extinction.

Neottioideae. This kladogenetic line is the most successful one, as well as the most important one in the whole family, for it provides all of the evidence necessary for the interpretation of the various evolutionary pathways that make the present-day complexity understandable. It was within the framework of this subfamily that evolutionary developments (or rather evolutionary innovations) leading to a secondary kladogenetic differentiation, EPIDENDROIDEAE, and opening all avenues toward a successful expansion in both structural diversity and spatial distribution, occurred.

The column in the NEOTTIOIDEAE and in the EPIDENDROIDEAE is strikingly dissimilar to those of the other subfamilies, although all share in common a certain degree of fusion between the style and the filament or filaments. Such a fusion must have occurred independently many times during the early history of the family, but only four kladogenetic lines have been carried through to the present. The single fertile anther is free and movably connected with the column at its acrotonic end.

A closer inspection of the hologeny of this subfamily, FIGURE 4 (5), seems to focus on the presence of two major anagenetic trends. One of these is expressed in the aggregation of free pollen grains into tetrads and the tetrads into pollinia, while the other can be traced in the progressive modification of one of the stigmatic lobes into a new organ called the rostellum. Although the interaction of these two trends seems to provide an inexhaustible reservoir for diversity, the true expansion of the orchid family owes its existence to the coaction of a third evolutionary innovation, the development of the epiphytic mode of life. The main anagenetic lines are designated here as tribe Cranichideae, tribe Neottieae, and tribe Epipogoneae.

Epidendroideae. The members of this subfamily are all advanced types. In regard to the development of floral parts, the EPIDENDROIDEAE represents the final stage in the organogenesis of the column, because there is a complete fusion of the reproductive organs in every species. Correlated with this fusion is a fully functional rostellum to which the pollinia are attached. There is also a further correlation between the position of the anther and the rostellum and between the position of the rostellum and structural changes in the pollinia (6). An inspection of longitudinal sections of developing flower buds, which are assembled according to their affinities in FIGURES 5 and 6, clearly shows that the

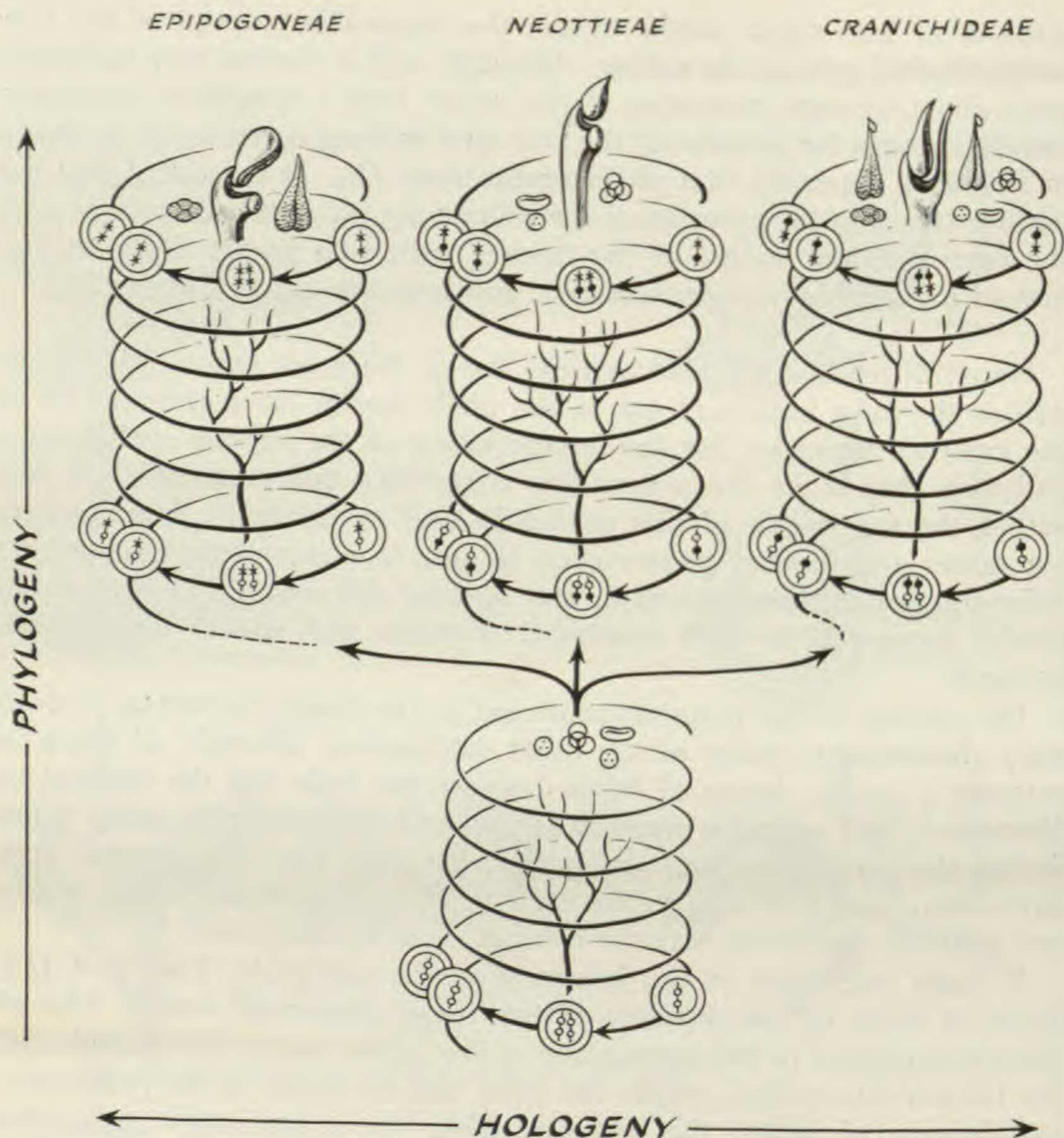


FIGURE 4. Phylogeny and hogeneity of subfamily NEOTTIOIDEAE.

various floral types fall within two anagenetic lines or natural evolutionary units: 1, column with an erect anther and an ascending (arrect) rostellum to which the pollinia are attached without appendages, and 2, column with an incumbent anther and a horizontally projecting (porrect) rostellum to which the pollinia are affixed through well-developed stipes. These two evolutionary lines are designated here as tribe Epidendreae and tribe Vandaeae respectively (6).

The columnar structure in the Epidendreae is very similar to that of the Cranichideae of the subfamily NEOTTIOIDEAE. Anagenetic differentiation in the NEOTTIOIDEAE is expressed in three distinct lines or natural evolutionary units (5). Because of the identity of the angle of the insertion of the anther and also of the ascending rostellum in both the Cranichideae and Epidendreae, I believe that the subfamily EPIDENDROIDEAE owes its existence to a secondary kladogenetic differentiation that took

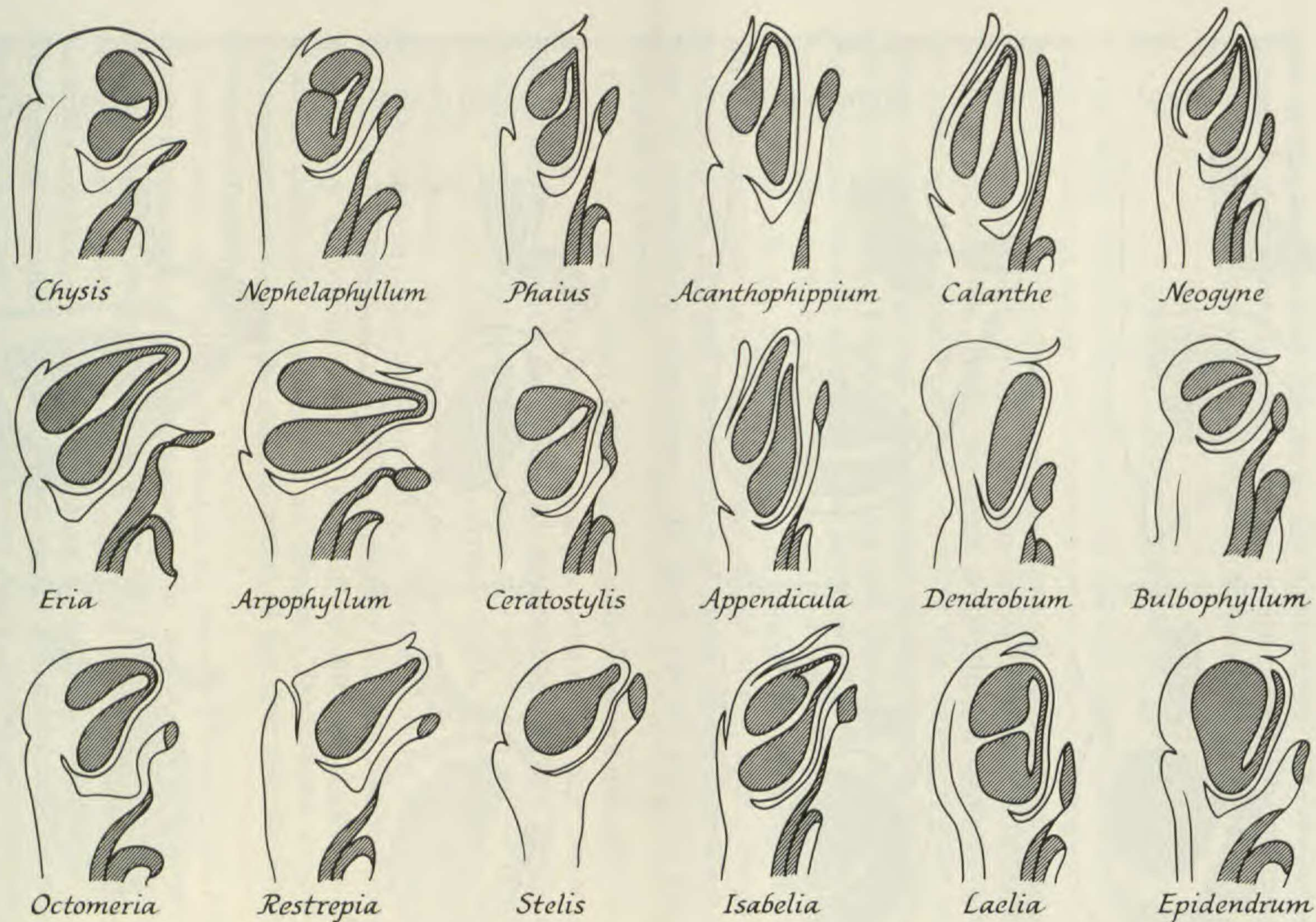


FIGURE 5. Diagrammatic median longitudinal sections of column in developing buds of members of tribe EPIDENDREAE.

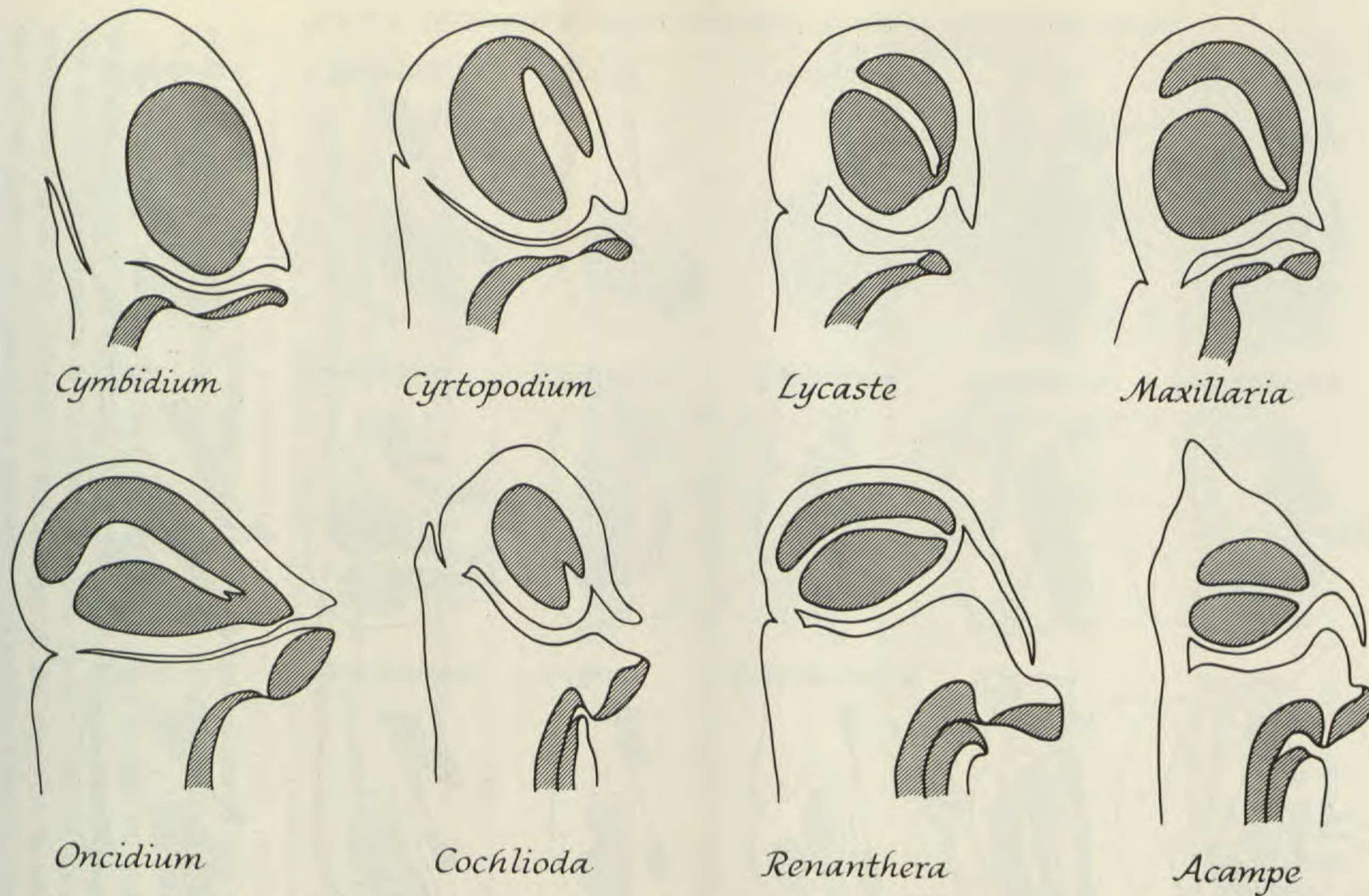


FIGURE 6. Diagrammatic median longitudinal sections of column in developing buds of members of tribe VANDEAE.

place in the early history and origin of the NEOTTIOIDEAE. Embryological evidence favors such a proposition, for the primitive type of embryo with a single-celled suspensor is found only in members of the Cranichideae and in the less evolved species of the Epidendreae. The evolutionary success of the EPIDENDROIDEAE, however, is due primarily to the development of the epiphytic mode of life, as has already been mentioned (6).

EVOLUTIONARY PERSPECTIVES

The family Orchidaceae originated in the area known phytogeographically as Malaysia during the Cretaceous period when most angiospermous families became differentiated. At that time all species were geophytes, for the epiphytic mode of life is a rather recent development, dating back to the Pliopleistocene. While the terms geophytic and epiphytic convey the meaning of ecological habitats, in reality they express distinct evolutionary adaptations through morphological modifications in the roots. In the terrestrial roots, which may be thin and fibrous or thick and fleshy, the epidermis consists of one to three layers of cells, the outermost layer being provided with root hairs. In the derived epiphytic roots, the layers of epidermal cells are greatly increased in number into a spongy velamen with the outermost layer cutinized and devoid of root hairs. Hence the structure of the root and not the place of abode differentiates these two types of evolutionary adaptations, the latter one of which is also an evolutionary innovation.

There is no other plant family comparable in floral diversity to the Orchidaceae. The basic trimerous pattern common to most monocotyledons, displays such a vast array of modifications in this family that without serious study one could question the validity of calling them all orchids. Yet, all of the flowers have three sepals and alternating with them three petals, the unpaired petal greatly modified into a labellum or lip, an evolutionary adaptation providing a landing platform for pollinating insects. In the center of the flower, ordinarily occupied by the style and encircled by alternating rows of stamens, all orchids possess a novel structure called the gynostemium or column. The column is also an evolutionary innovation, the result of fusion of the style with the filaments of various stamens.

Concurrently with the development of the column two additional evolutionary innovations became operational. The first is the development of pollinia, in which the pollen grains at the time of maturity are shed either as free single grains, or variously aggregated into tetrads or massulae. Each of these phases is very characteristic for a given subfamily (4, 5, 6). The manner in which the individual grains are united into tetrads or massulae is a unique feature of the orchid family, for the interfaces among the grains instead of becoming separated by an exine layer remain connected through cytoplasmic plasmodesmata. Because of this phenomenon cytogenetically deficient grains are brought to maturity, and in turn can affect fertilization (1). This condition is amply demonstrated by the

occurrence of large aneuploid series, a source of variation, especially in the subfamily EPIDENDROIDEAE and the more advanced members of the NEOTTIOIDEAE (5, 6).

The kind of pollinia, that is, the stage of the aggregation of pollen grains, is the very factor that determines the population size and the spatial distribution of the individuals of each species. In the subfamilies APOSTASIOIDEAE, CYPRIPEDEOIDEAE and NEOTTIOIDEAE both are rather limited. However, in the EPIDENDROIDEAE in the final stage of evolution of pollinia into firm, compact massulae, permitting the pollinating vectors to carry them over great distances, spatially extensive populations appear as the rule rather than the exception.

Yet, the success of this mechanism in regulating as well as maintaining the population-size is closely tied in with the second additional evolutionary innovation referred to above, namely the alteration of one of the stigmatic lobes into a new organ, the rostellum. The rostellum produces either a viscous secretion or a viscous gland to which the pollinia are attached. It is, therefore, a device that ensures successful cross pollination by firmly anchoring the pollinia to vectors for transportation. This evolutionary modification is observable in the more advanced members of the NEOTTIOIDEAE and in the subfamily EPIDENDROIDEAE. There is no rostellum in the APOSTASIOIDEAE, CYPRIPEDEOIDEAE and ORCHIDOIDEAE (6).

In addition to anchorage, the rostellum also serves as a device that prevents self pollination. In a few species, however, if the flower is not visited by a pollinator, at the end of anthesis the rostellum dries up, thus allowing the pollinia to come into contact with the stigma and permitting self pollination (5).

Orchids are pollinated by a large variety of insects, especially bees, flies, wasps, butterflies and moths, as well as by hummingbirds. Ordinarily the pollinator is species specific. Undoubtedly, cross pollination is merely a by-product of the insect's activity when attracted by a flower and stimulated to satisfy one of the ever-present dynamic urges of nature: hunger or sex. While the flowers of most orchid species provide either nectar or edible tissue as an attractant for the visiting insect, there are a few which successfully mimic the female species of the pollinator, thus attracting them sexually. Recognition of this unusual orchid-insect association which results in pseudocopulation, is a relatively recent addition to our knowledge of orchidology, yet the phenomenon itself must be of long standing in the evolutionary history of the family. Although in the annals of orchidology a large number of descriptive cases of individual pollinating mechanisms are recorded, the value of these observations and their evolutionary implications will be first realized when the mutual coaptations between flowers and insects and the reciprocal modifying influence on their evolution are convincingly demonstrated.

The evolutionary innovations discussed above, and their mutual interactions to a large extent explain the origin of, and present-day diversity within, the family. However, the dispersal of sundry orchid diaspores has played an equally important role in bringing about this diversity, especially

when it was followed by some type of isolation. The common isolating barriers among orchid species are physiological, ecological, ethological, or geographic and relatively seldom genetic. This observation is corroborated by literally thousands of artificial hybrids, often between remotely related species, as well as by the occurrence of natural hybrids. The relative frequency of natural hybrid populations of orchids in the subfamily EPIDENDROIDEAE is an additional indication of the rapid evolutionary expansion that took place within a less rigid framework than would be possible with genetic incompatibility as a controlling force. Hybridity whether natural or artificial can occur only within a given subfamily. The lack of genetic compatibility between species belonging to different subfamilies, even in artificially attempted crosses, seems to support the thesis that the kladogenetic differentiation into five subfamilies must indeed have taken place shortly after the family came into existence (6).

Closely associated with the initial kladogenetic differentiation of the orchid family is its early expansion and global dispersal. Continental distribution patterns are usually intimately associated with the geologic, climatic, and edaphic history of a given area, hence their explanation is rarely problematic. Transoceanic dispersals, on the other hand, are more perplexing, for the causes often are hidden in the evolutionary past of our biosphere (7).

There are approximately 800 genera recognized in the orchid family, and of these only 32 can now be identified as being involved in some kind of oceanic distribution. It is significant that 27 of the 32 taxa, i.e. 85 percent, are genera whose members are exclusively terrestrial. Epiphytic orchids are less habitat-specific in the microenvironment than terrestrials, yet we know only two such genera, *Bulbophyllum* and *Polystachya*, with a pantropical range. This situation, however, does not suggest that terrestrials are more effectively dispersed than epiphytes; it merely indicates that the initial transoceanic expansion must have taken place shortly after the family became established and before the epiphytic mode of life evolved. Since all of the early species were terrestrials, the transoceanic dispersal of epiphytes, although following the same route as the terrestrials did, was of much later occurrence. The necessity of mycorrhizal association is a well-known factor in orchids, but this association is not species specific. This requirement is more readily met in soil conditions where an ample supply of decaying organic matter is available than on exposed branches of trees. Hence, this is another contributing factor accounting for the rather sparse transoceanic dispersal of epiphytes (7).

Orchid genera, whether restricted to adjacent continents or pantropical in range, have the origin of their phyletic affinities in Malaysia (4, 5, 7): this center of origin must not be confused with the actual center of distribution, since the two types of centers may not be identical. In general the migratory expansion or dispersal proceeded from an easterly to westerly direction from Malaysia-India-Madagascar-Africa to Africa-South America. The exception to this is the transpacific route between Malaysia and South America as exemplified by the genera *Tropidia* and *Erythrodes*.

The migratory routes through which the various orchid dispersals were accomplished are amply documented in the pages of phytogeographical literature. They rather convincingly demonstrate that dispersals took place via oceanic routes by island-hopping rather than through supposed continental highways. There is no definite evidence that land connections of a continental nature were in existence during the Tertiary, when most of the transoceanic dispersals took place. Furthermore, geomorphological and oceanographic evidence indicates that the earth is in a constant flux and was even more so in the past. The subsidence of the ocean floor and the fluctuation of the sea level during the various geological periods, combined with orogenic activities in the earth's crust, have provided time and again favorable avenues between continents for transoceanic dispersals by means of island-hopping. In addition to these factors, wind currents have also played an important role in the transportation of orchid diaspores. In that, the "intertropical convection current" (doldrums) must have at least partially aided the realization of transoceanic distributions, for the observed distribution patterns of orchids, for instance, that of *Liparis nervosa*, and that of the intertropical convection current coincide remarkably well (7).

EPILOGUE

In spite of our attempt to view the progressive evolution of the *Orchidaceae* from a transpecific level, it always took place within specific levels. Theoretically, along the path of progressive differentiation, the newly formed types or species were much improved over their ancestors. However, even if we admit Darwin's statement that all "recent species have proved their superiority over their extinct ancestors by their survival," we must remember that this superiority does not necessarily represent progressive evolution, i.e., anagenesis. During the process of specialization, natural selection usually causes progressive adaptation to special conditions of the environment and this adaptiveness may turn into a fatal disadvantage in future development, because of the lack of ability to cope with radical environmental changes. It is for this absence of general versatility that lines with progressive specialization are frequently and ultimately doomed to extinction, notwithstanding the "superiority" of each subsequent type over the ancestral form.

The story of the evolution of the orchid family is deeply anchored in this phenomenon of extinction concerning which the present-day species with their great diversity, highly specialized and modified structures, and genetic complexities afford us only a dim view.

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